Influences of recovery from clear-cut, climate variability, and thinning on the carbon balance of a young ponderosa pine plantation

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Abstract

From 1999 to 2002, the variations in carbon flux due to management practices (shrub removal, thinning) and climate variability were observed in a young ponderosa pine forest originated from clear-cutting and plantation in 1990. These measurements were done at the Blodgett Forest Ameriflux site located in the Sierra Nevada Mountains of California. Thinning in spring 2000 decreased the leaf area index (LAI) by 34% and added 496 g C m^{-2} of wood and leaf debris at the soil surface. Total ecosystem respiration was not significantly affected by thinning (1261 g C m^{-2} in 1999 and 1273 g C m^{-2} in 2000), while canopy photosynthesis decreased by 202 g C m^{-2}. As a result the ecosystem shifted from a net sink of CO_2 in 1999 (-201 g C m^{-2}) to a small net source in 2000 (13 g C m^{-2}). Woody and leaf debris resulting from thinning only accounted for maximum 1% and 7% of the total respiration flux, respectively. Thinning did not affect the relative proportion of the different components of respiration to an observable degree. Low soil water availability in summer 2001 and 2002 decreased the proportion of soil respiration to the total respiration. It also imposed limitations on canopy photosynthesis: as a result the ecosystem shifted from a sink to a source of carbon 1 month earlier than in a wetter year (1999). The leaf area index and biomass of the stand increased rapidly after the thinning. The ecosystem was again a sink of carbon in 2001 (-97 g C m^{-2}) and 2002 (-172 g C m^{-2}). The net carbon uptake outside the traditionally-defined growing season can be important in this ecosystem (NEE = -50 g C m^{-2} in 2000), but interannual variations are significant due to differences in winter temperatures.

1. Introduction

Variations in net ecosystem carbon exchange (NEE) between sites has been attributed largely to disturbance history, with important secondary effects

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from site climate, vegetation ecophysiology, changing atmospheric CO_2 and nitrogen deposition (Thornton et al., 2002). Full ecosystem carbon accounting requires consideration of these disturbances (Meroni et al., 2002; Saleska et al., 2003). Schelhaas et al. (2003) estimated that natural disturbances, mostly wind storms and fires, accounted for ~8% of the total felling of trees in Europe over the past 50 years, making harvesting through clear-cut and thinning by far the most important disturbance factor.

At a global scale 44% of the world's forest are managed, and thus, subjected to some sort of silviculture (FAO, 2000). Amongst the silvicultural practices, thinning is one of the most common treatments applied by foresters to deliver wood for commercial purposes, while decreasing competition between the remaining trees. In the Sierra Nevada forests of California, the objectives of thinning include timber harvest, tree growth redistribution, tree species regulation, wildlife habitat improvement, and wild-fire-hazard reduction (Graham et al., 1999). Wildfires have become more severe because stand biomass and shade-tolerant understory have increased due to fire suppression over the past 80 years (Mutch, 1994). In the western United States, thinning is being con-sidered at large spatial scales for forests that are overstocked and prone to wildfire. The Sierra Nevada Forest Plan Amendment has been reformed recently to authorize thinning of 32,000 ha a year, removing 25% of the total annual growth over 4.6 millions of hectares in 11 National Forests (USDA, 2004).

The impact of thinning on tree-growth has been widely studied (e.g. Assmann, 1970; Breda et al., 1995; Misson et al., 2003), yet only a few studies provide results on the effects of thinning on above-ground net primary productivity (NPP) (Coops, 1999; Mitchell et al., 1996; Mund et al., 2002). Despite its importance, there is still a lack of published studies concerning the impacts of partial disturbances on NEE. To the best of our knowledge, there are no published studies of the effect of thinning on the total carbon balance between the forest and the atmosphere. Comparative and process studies about such distur-bances are required to address this issue, including ecosystem manipulation experiments that provide the necessary information to develop and validate terrestrial biosphere models (Canadell et al., 2000; Geider et al., 2001; Schimel et al., 1997).

In this paper, we report a 4-year case study (1999–2002) of carbon flux measured continuously before and after thinning a young ponderosa pine plantation growing in a semi-arid environment in the Sierra Nevada Mountains of California. The main objective of our analysis is to quantify the ecosystem carbon flux and how it changes following common management practices applied in this region. We also examine the seasonal and interannual variation in carbon exchange in relation to climate variability.

2. Materials and methods

The Blodgett Forest site and ongoing measure-ments have been extensively described (Goldstein et al., 2000; Xu et al., 2001; Tang et al., 2005). Here, we will focus on the important characteristics relevant to this paper.

2.1. Site description

The study site is part of the Ameriflux and Fluxnet networks. It is located (38°53′42.9″N, 120°37′57.9″W) at 1315 m above sea level in the Sierra Nevada Mountains of California, adjacent to the Blodgett Forest Research Station, a research forest of the University of California at Berkeley. Trees were planted in 1990 at a density of ~1200 trees/ha. The plantation (~20 ha) is dominated by ponderosa pine (*Pinus ponderosa* L.) with occasional other tree species. The major understory shrubs are *Arctosta-phylos manzanita* (Mazanita) and *Ceonothus cordu-latus* (Ceanothus). In spring 1998 about 58% of the ground area was covered by trees, 24% by shrubs, and the remaining 18% was grass, stumps and bare soil. In spring 2000 mean tree DBH was 6.2 cm, mean tree height was 2.9 m, and basal area was 6.3 $m^{-2} ha^{-1}$.

The site is characterized by a Mediterranean climate, with warm dry summers and cold wet winters. Since 1998, annual precipitation has averaged 1290 mm, with the majority of precipitation falling between September and May, and almost no rain in summer. Daily mean air temperature ranged from 14 °C to 27 °C during summer and from 0 °C to 9 °C during winter. The soil has 60% sand and 29% loam with a pH of 5.5 ± 0.29. In 1998, the top 30 cm of soil contained 6.9% organic matter and 0.17% nitrogen.

2.2. Management practices

Shrubs were removed in June 1999. They were manually cut at the base of the trunk using hand tools and left on site to decompose. The plantation was thinned in 2000 between May 11th and June 15th, when the trees were 10-year-old. Thinning was accomplished with a masticator (CDF, 2002), consisting of a backhoe-type vehicle with an articulating arm. On the end of the arm was a rotating blade that chopped woody vegetation from the top down, turning woody material into mulch that was left on the ground to decompose. Mastication is becoming a more widespread method for precommercial thinning in the USA, because the trees that are cut are almost universally left on the site, and mastication of the thinned trees is one way to reduce fire hazard (CDF, 2002).

2.3. Eddy covariance measurements

Continuous year round measurements started in spring 1999. These measurements have been extensively described in Goldstein et al. (2000). Wind velocity and sonic virtual temperature fluctuations were measured at 10 Hz with a three-dimensional sonic anemometer (ATI Electronics Inc., Boulder, CO, USA) mounted on a horizontal beam at 10.5 m above the ground. CO_2 and H_2O mixing ratios were measured with closed path infrared gas analyzer (LI-6262, Li-Cor Inc., Lincoln, NE, USA). The raw analog data provided response times of 10 Hz for both gases. Additionally the canopy vertical profiles of CO_2 and H_2O mixing ratios were measured every 30 min (LI-6262, Li-Cor Inc., Lincoln, NE, USA) by sampling sequentially at 5 heights for 6 min each.

Negative fluxes indicate mass and energy transfer from the atmosphere to the vegetation. Data presented in this paper include the continuous period from spring 1999 through the end of 2002. The sonic anemometer wind data was rotated to force the mean vertical wind speed to zero, and to align the horizontal wind speed onto a single horizontal axis. The time lag for sampling and instrument response was determined by maximizing the covariance between vertical wind velocity (w') and scalar (c') fluctuation. Errors due to sensor separation and damping of high frequency eddies were corrected using spectral analysis techniques as outlined by Rissmann and Tetzlaff (1994). Storage corrections were applied to the fluxes of CO_2 in order to avoid flux underestimation (Aubinet et al., 2000).

Energy balance closure for this ecosystem has been tested by comparing the sum of measured half-hourly energy fluxes (latent + sensible + soil heat fluxes; $LE + H + G$) to the net radiation measured above the canopy (R_n). This comparison suggested an imbalance ranging from 12% (1999) to 16% (2001). These values are in the lower range of imbalances reported in studies using the eddy-covariance method within the Fluxnet network (10–30%, with an average of 20%) (Wilson et al., 2002).

2.4. Meteorology

Environmental parameters were recorded every 5 s and 0.5 h average were calculated and stored on a CR10X datalogger (see Goldstein et al. (2000) for description of all instruments). The parameters included wind direction and speed, vertical profiles of wind speed at 3 heights, vertical profiles of air temperature and humidity in aspirated radiation shields at 4 heights, net radiation, photosynthetically active radiation, soil temperature in three locations at 5, 10, 15, 30 and 50 cm depths, soil moisture at 10, 30 and 50 cm depths, soil heat flux at three locations, rain, and atmospheric pressure.

In order to compare mean fluxes under different meteorological conditions across the measurement years, four-time periods, each of 40 days, were chosen to divide the years into different precipitation, soil moisture and air temperature regime (Fig. 1). The first period (p1, spring) included days from June 9 to July 19 and was characterized by medium soil water content and cool air temperature (Fig. 1). The second period (p2, summer) included days from July 19 to August 28 and was characterized by low soil water content and high temperature. The third period (p3, fall) included days from September 17 to October 27, when strong drought stress usually developed due to lack of rainfall. The fourth period (p4, winter) included days from November 16 to December 26 and was characterized by high moisture content and low temperature.

2.5. Soil respiration

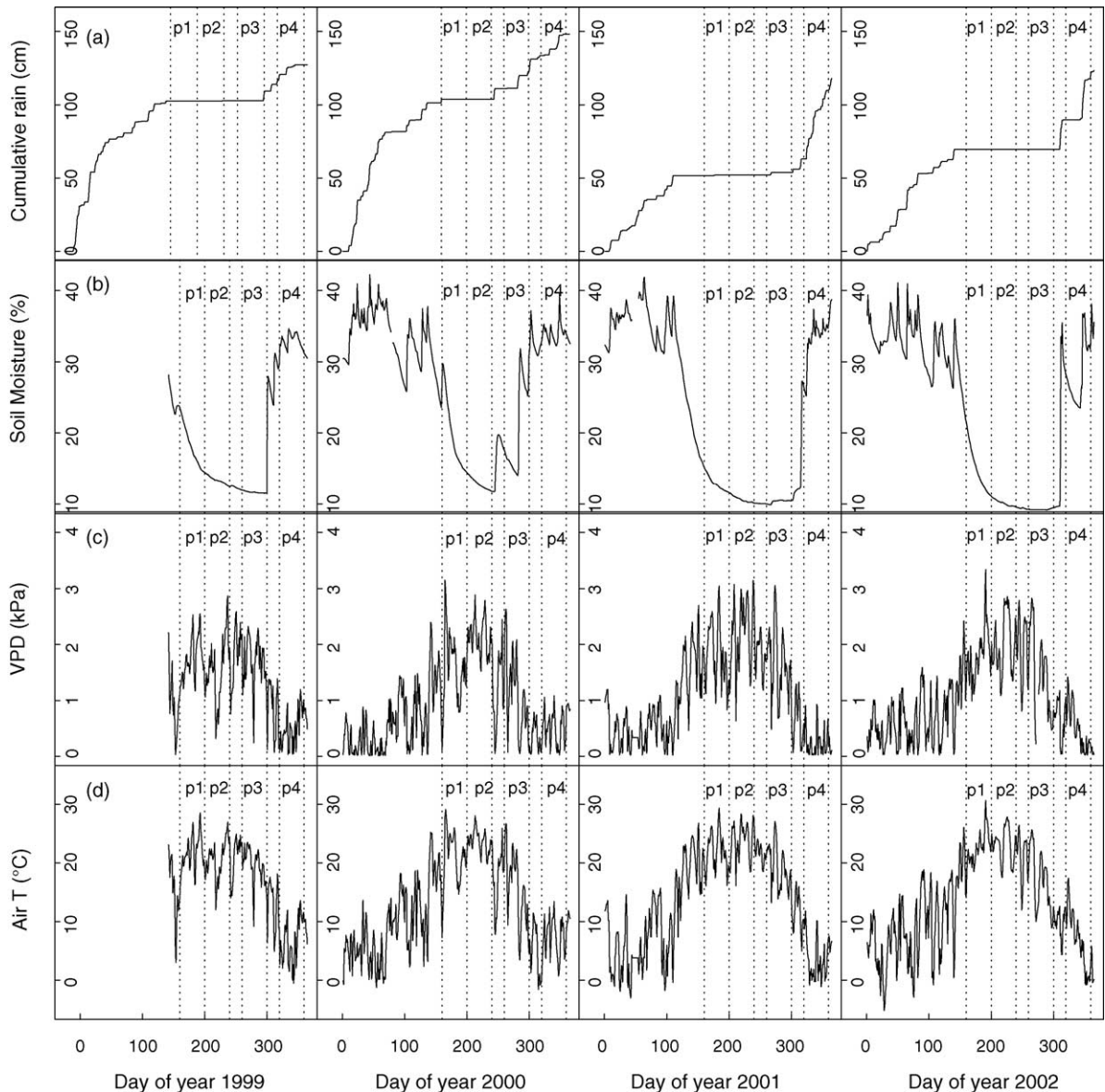These measurements have been extensively described in Tang et al. (2005). We established

Fig. 1. Meteorological variables: (a) cumulative sum of rain, (b) soil moisture content at 10 cm depth, (c) mean midday (10:00–14:00) vapor pressure deficit and (d) mean midday (10:00–14:00) air temperature. Vertical lines separate the averaging periods for analysis of the fluxes (see text).

two 20 m × 20 m sampling plots separated by 40 m in the middle of the tower footprint. In each plot, soil CO_2 efflux and soil temperature at 10 cm depth were measured on a 3 × 3 matrix at 10 m spacing, resulting in 18 measurement locations. A soil collar, with a height of 4.4 cm and a diameter of 11 cm, was permanently inserted into the soil at each sampling point. Soil CO_2 efflux was measured using an LI6400-09 soil chamber connected to an LI-6400 portable photosynthesis system (Li-Cor Inc., Lincoln NE, USA). The measurement of soil CO_2 efflux started in June 1998. Soil CO_2 efflux measurements were conducted during 1 or 2 days every month, except during winter when snow covered the ground.

Each sampling location was measured 8–10 times per sampling date.

2.6. Litter-bag analyses

Litter decomposition was measured using 15 cm × 20 cm litter-bags made of fiberglass window screening with 1 mm mesh. We constructed 220 litter-bags containing pine needles, 150 bags containing Manzanita leaves and 24 bags containing coarse woody debris. We used 2-year-old ponderosa pine live needles and 1-year-old Manzanita live leaves. The needles/leaves were air dried for 2 weeks prior to filling the litter-bags. Woody material was collected from the dead branches of ponderosa pine trees. The woody material was air dried for 1 month before filling the litter-bags. In June 1998, the needle/leaf litter-bags were placed near all 18 locations where we measured soil respiration, while the woody litter-bags were placed at centers of both sampling plots. For coarse woody debris a subset of the bags was retrieved every month in the following 5 months, then every 5 months in the following 2 years. The leaf litter-bags were retrieved in May 1999. The retrieved litter-bags were oven dried at 70 °C for 48 h and weighed to determine the decomposition rate.

2.7. Dendrometric measurements

Since 1997, tree height, diameter at breast height, crown width and percentage of cover for the different species were measured each year at the end of the winter along a transect composed of twenty continuous 10 m × 10 m plots. This transect is located in the tower footprint. These parameters were also measured just after thinning in spring 2000 in order to estimate the biomass and leaf area index (LAI) masticated during this operation. During the growing season, new needle and shoot elongation were measured every week on three randomly chosen trees, with good agreement between these measurements. The stem and branch biomass of the trees were calculated using allometric equations developed for our site and published in Xu et al. (2001). From the biomass we also derived the sapwood surface assuming that the stem has a conical shape (Xu et al., 2001). The LAI for the different needle age classes was calculated from allometric equations presented in Xu et al. (2001), and was transformed into mass using the specific leaf area parameter (leaf area per unit dry mass, all-sided SLA old needles = 90 cm^2 g^{-1}, all-sided SLA new needles = 81 cm^2 g^{-1}). The evolution of LAI and sapwood area during the growing season was reconstructed by assuming that the dynamics of leaf and sapwood area growth followed needle elongation, similarly to Xu et al. (2001). Before 2002, there was no appreciable growth of shrubs. In summer 2002, the shrubs started to grow vigorously and their LAI was measured during the winter by destructive sampling outside of the flux footprint (Fig. 2d).

2.8. Respiration model and gross ecosystem productivity

Most of the time, daytime turbulence was strong enough to produce reliable eddy covariance flux measurements (friction velocity > 0.2 m s^{-1}). During night, conditions were consistently much calmer causing the eddy covariance flux measurements to be less reliable. This limitation made it inappropriate to use nighttime eddy-covariance measurements to estimate respiration flux. We therefore modeled ecosystem respiration based on field measurements of leaf, bole and soil respiration. During night, NEE data was replaced by modeled ecosystem respiration. Leaf respiration (R_{leaf}) was modeled as function of temperature using equations developed specifically for our site (Goldstein et al., 2000; Xu et al., 2001; Xu and Qi, 2001):

$$R_{leaf} = LAI\, a \exp\left[b(T_{leaf} - T_{ref})\right] \tag{1}$$

where R_{leaf} is ecosystem scale leaf respiration (μmol m^{-2} s^{-1}); LAI, the leaf area index (m^2 m^{-2}); T_{ref}, a reference temperature (10 °C); and T_{leaf}, the leaf temperature which for this model is considered equal to air temperature (°C). The parameters a and b were empirically fitted to dark respiration measurements for both old ($a = 0.17$ and $b = 0.047$) and new needles ($a = 0.17$ and $b = 0.090$). Based on the biomass data presented in Xu et al. (2001), we calculated that LAI for new and old needles were, respectively, 48% and 52% of total stand LAI. Leaf respiration from shrubs was calculated using the parameters derived for old ponderosa pine needles as in Xu et al. (2001). Bole
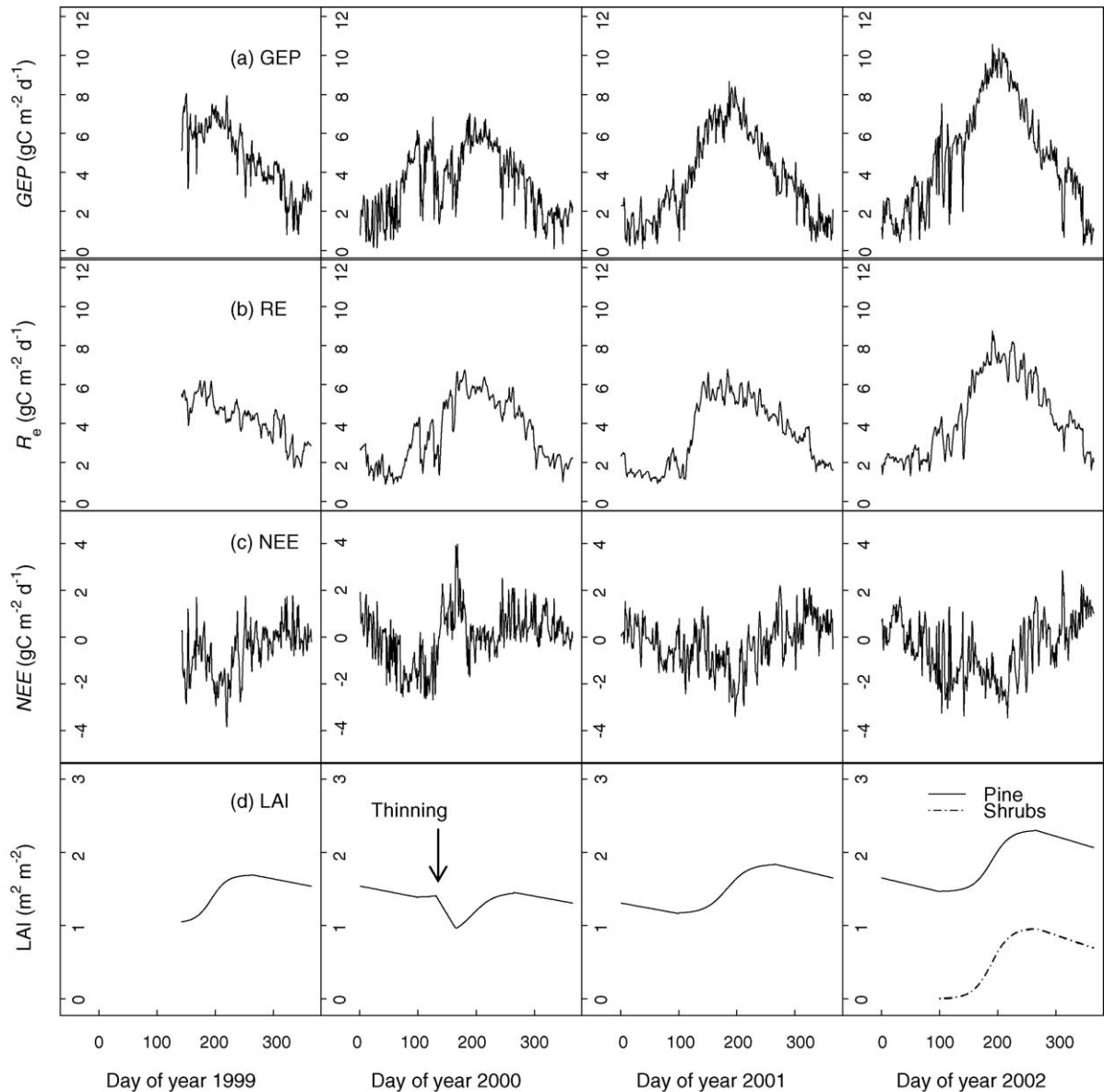
Fig. 2. Daily values of (a) GEP, (b) R_e, (c) NEE, (d) LAI for ponderosa pine and shrubs from 1999 to 2002 (for all-sided ponderosa pine LAI multiply by 2.3).

respiration was calculated following Goldstein et al. (2000):

$$R_{\text{bole}} = \text{SAI}\, c \exp\left(d\, T_{\text{soil,5}} + e\right) \qquad (2)$$

where R_{bole} is ecosystem scale bole respiration (μmol m^{-2} s^{-1}); SAI, the sapwood area index (sapwood surface area per unit surface area of soil,

m^2 m^{-2}); $T_{\text{soil,5}}$, the soil temperature at 5 cm depth ($^\circ$C); and c, d and e were empirically fitted parameters ($c = 0.085$, $d = 0.057$, $e = 0.17$). Soil respiration, including leaf decomposition from mastication, was calculated from equations recently published in Tang et al. (2005):

$$R_{\text{soil}} = f \exp\left(g T_{\text{soil,10}}\right)\exp(h\theta_v - i\theta_v^2) \qquad (3)$$

where R_{soil} is ecosystem scale soil respiration (μmol m^{-2} s^{-1}); $T_{\text{soil,10}}$, the soil temperature at 10 cm depth (°C); and θ_v, the volumetric soil water content at 0–30 cm depth (m^3 m^{-3}). Parameters f, g, h and i were empirically fit independently for the data before and after thinning (before thinning $f = 0.317$, $g = 0.0439$, $h = 0.2$, $i = 0.00506$; after thinning $f = 0.277$, $g = 0.0439$, $h = 0.2$, $i = 0.00506$; in 2002 $f = 0.297$, $g = 0.0439$, $h = 0.2$, $i = 0.00506$). Shrub removal, thinning and mastication produced leaf and coarse woody debris. Leaf debris decomposition was included in measurements of soil respiration and therefore also in the model (Eq. (1)). Decomposition of leaf and coarse woody debris was calculated based on litter-bag data using a simple linear decay model (Lambert et al., 1980; Wieder and Lang, 1982):

$$R_{\text{leaf decay}} \text{ and } R_{\text{wood decay}} = kX_0 \qquad (4)$$

where $R_{\text{leaf decay}}$ and $R_{\text{wood decay}}$ are decomposition flux (g C m^{-2} y^{-1}); k, the decay rate (fraction of mass loss y^{-1}); and X_0, the initial biomass. Total ecosystem respiration (R_e) was calculated daily and yearly as the sum of leaf, bole, soil and coarse woody debris respiration:

$$R_e = R_{\text{leaf}} + R_{\text{bole}} + R_{\text{soil}} + R_{\text{wood decay}} \qquad (5)$$

Gross ecosystem productivity (GEP) was calculated as the difference between ecosystem respiration (R_e) and NEE:

$$\text{GEP} = R_e - \text{NEE} \qquad (6)$$

2.9. Light and water use efficiency

Canopy water use efficiency (WUE, mmol mol^{-1}) was computed as the ratio of net CO_2 uptake ($-$NEE, mmol m^{-2} s^{-1}) over water vapor flux (mol m^{-2} s^{-1}). This is the ratio of net carbon fixed by the ecosystem per amount of total water loss to the atmosphere. Mean midday values (10:00–14:00) were computed and averaged for different periods of the year.

Canopy light use efficiency (ε_c, a measure of the efficiency of the foliage for using incoming radiation to assimilate CO_2) was computed as:

$$\varepsilon_c = \frac{\text{GEP}}{\text{APAR}} \qquad (7)$$

where GEP is gross ecosystem productivity (mol m^{-2} s^{-1}), and APAR is absorbed photosynthetically active radiation (mol m^{-2} s^{-1}). APAR was computed as:

$$\text{APAR} = (1 - \alpha_c)\text{PAR}[1 - \exp(-k\text{LAI})] \qquad (8)$$

where α_c is canopy albedo (0.067, dimensionless); PAR, the photosynthetically active radiation (mol m^{-2} s^{-1}); and k, the canopy light extinction coefficient (0.5, dimensionless).

2.10. Gap-filling strategy

Missing data are unavoidable due to instrument malfunctions, power failures, or bad statistics of turbulence parameters. Overall we missed 14% of the daytime flux data during the measurement period in 1999 and 9% in 2000, 2001 and 2002. Missing data was typically more prevalent during the winter ($\sim$30%) than during the summer ($\sim$5%) due mainly to wet conditions when the sonic anemometer could not function properly. Over the 4 years of data reported here, the maximum amount of missing data in 1 month occurred in February 2001 (51%). We used several procedures to fill the gaps in order to determine annual sums of carbon fluxes. For blocks of 1/2 h or 1 h of missing data, a linear interpolation method was used. Larger blocks of daytime missing data were filled using the following response function:

$$\begin{aligned} \text{NEE} &= c\exp(qT_{\text{air}}) \\ &\quad - \left(\frac{P_{\text{max}}\alpha Q_p}{P_{\text{max}} + \alpha Q_p}\right)\left(\frac{1}{1 + (\text{VPD}/\text{VPD}_0)}\right) \end{aligned} \qquad (9)$$

where T_{air} is air temperature (°C); P_{max} (mmol m^{-2} s^{-1}), the maximum canopy photosynthesis at infinite light; α, the apparent quantum yield; Q_p (mmol m^{-2} s^{-1}), the incident photosynthetically active radiation; and VPD, the atmospheric vapor pressure deficit (kPa). The parameters c, q, P_{max}, α and VPD_0 were fitted empirically using a nonlinear fitting procedure. Because of the seasonality in phenology and meteorological control of NEE, we used 1-month time windows to fit these parameters and then filled any data gaps within that month. Sometimes the fitting procedure gave a nonsensical estimate for c, q, or VPD_0 parameters (i.e. estimate inconsistent with the observed data). In this case, a value was assigned to

this parameter and the response function was fitted again. Percent variations in NEE that can be explained by Eq. (9) varied between 30% and 83%.

Since the continuous eddy-covariance measurements did not start until spring 1999, we missed the first 4 months of data for this year. Gap filling using Eq. (9) is not possible for such a long period. However, meteorological conditions during this period were similar with conditions reported for the first part of the year 2000 (Fig. 1): average daily temperature differed by 2.7 °C, average daily relative humidity by 1% and total precipitation by 10 mm. LAI was also similar, with value around 3.1 $m^2 m^{-2}$ during winter 1999 and 3.45 $m^2 m^{-2}$ during winter 2000. Given the similarity of weather and LAI, NEE for the first part of the year in 2000 (prior to thinning) could be a good approximation of NEE for the same period in 1999. We, thus, filled the gap of NEE in 1999 by using data in 2000 prior to thinning in order to compare the 2 years (Table 2).

Almost all meteorological variables required for this analysis were recorded using several sensors that were intercalibrated, so a continuous time series was nearly always available. For small blocks of missing data, a linear interpolation method was used. For larger gaps, we used intercalibrated data recorded at a nearby weather station (~2 km) at the Blodgett Forest Research Station.

3. Results

3.1. Meteorology

The total annual precipitation was 1273 mm in 1999, 1481 mm in 2000, 1178 mm in 2001 and 1233 mm in 2002. The rainfall pattern was rather similar for the two wetter years (1999, 2000) with high precipitation from January to May, then no precipitation in spring (p1) or summer (p2) (Fig. 1). However, rainfall started earlier in fall 2000 than in 1999. The two drier years (2001, 2002) also had a similar pattern of rainfall with low precipitation from January to May, equal to ~60% of the total precipitation from the preceding years during the same period. Then no rainfall was recorded from spring to fall (p1 to p3) 2001 and 2002. In 2001, an extended 6.5-month dry period occurred with no rain from mid-April through

the end of October. In 2001 and 2002, soil moisture during fall dropped down to extremely low values (below 10%). Air temperature and vapor pressure deficit (VPD) followed very similar patterns across the years, with the highest values during spring (p1) and summer (p2), and large sub-weekly variation due to the passage of weather fronts (Fig. 1).

3.2. Leaf area index, thinning and mastication

Shrub removal during spring 1999 eliminated 0.8 $m^2 m^{-2}$ of LAI (one-sided), roughly half Manzanita and half Ceanothus. Based on the SLA for these two species (Manzanita = 41 $cm^2 g^{-1}$ and Ceanothus = 67 $cm^2 g^{-1}$), we estimated that 157 g C m^{-2} of leaves were left on the soil surface to decompose. Litter-bags containing the leaves of Manzanita decomposed at a rate of 39.4% y^{-1}.

The LAI (one-sided) of ponderosa pine increased from 1.0 $m^2 m^{-2}$ to 1.7 $m^2 m^{-2}$ during the 1999 growing season, then decreased to 1.4 $m^2 m^{-2}$ as the oldest needles fell during fall and winter (Fig. 2d). In spring 2000, LAI decreased from 1.4 $m^2 m^{-2}$ to 0.9 $m^2 m^{-2}$ during pre-commercial thinning of the plantation (Fig. 2d). LAI increased back to the pre-thinning level (~1.5 $m^2 m^{-2}$) by the end of the 2000 growing season. Net increases of LAI in 2001 and 2002 were 0.34 $m^2 m^{-2}$ and 0.45 $m^2 m^{-2}$, respectively. From spring 1999 (shrub removal) to the end of 2000, the shrubs were non existent. In 2001 they were a negligible component of the ecosystem. In 2002, they began to grow vigorously again and their LAI reached 0.7 $m^2 m^{-2}$ at the end of the year (Fig. 2d).

During thinning 60% of the trees were masticated, accounting for 34% of the LAI and 31% of the basal area because only the small trees were removed by this operation (Table 1). The thinned biomass was left on site to decompose, including 376 g C m^{-2} of stem debris and 120 g C m^{-2} of leaf debris (total = 496 g C m^{-2}). Litter-bags containing needles and coarse woody debris from ponderosa pine decomposed at rates of 25.9% y^{-1} and 4% y^{-1}, respectively.

3.3. GEP and R_e

Thinning in spring 2000 strongly affected GEP and R_e: both canopy photosynthesis and respiration decreased abruptly just after the thinning, with a

Table 1
Stand characteristics before thinning and impact of thinning

	Before thinning	Thinned	Thinned (%)
$N \, ha^{-1}$	1275	765	60
LAI ($m^2 \, m^{-2}$)	1.39	0.47	34
Leaf mass (g m^{-2})	354	120	34
Stem mass (g m^{-2})	1239	376	30
Stem volume ($m^3 \, ha^{-1}$)	29.49	8.96	30
Stem surface ($m^2 \, m^{-2}$)	0.85	0.20	24
Basal area ($m^2 \, ha^{-1}$)	6.30	1.98	31

$N \, ha^{-1}$: number of trees per hectare, LAI: leaf area index (one-sided, for all-sided multiply by 2.3).

stronger impact on the photosynthesis flux (Fig. 2a and b). Both fluxes remained altered for approximately 2 months before recovering. Thinning had only a slight impact on nighttime NEE (Fig. 3), which is governed by ecosystem respiration. On the other hand, thinning greatly increased daytime NEE, which is the difference between ecosystem respiration and canopy photosynthesis (Eq. (8) and Fig. 3). Thinning clearly had a greater impact on GEP than on R_e.

Thinning did not considerably change R_e and its different components (R_{leaf}, R_{bole}, R_{soil}, $R_{wood \, decay}$, $R_{leaf \, decay}$) between 1999 and 2000 (Table 2). In 2001, total respiration was almost similar to the preceding years but the distribution amongst the components was different: aboveground respiration increased and belowground respiration decreased, while soil moisture dropped to very low content (below 10%). In 2002, total respiration was much higher (+340 g C m^{-2}) than the preceding years. In 2002 soil respiration still represented a lower proportion of total respiration in comparison to 1999 and 2000, while soil moisture

content was very low during summer and fall (below 10%) (Table 2).

Based on the litter-bag data, we estimated that woody debris decomposition accounted for 1% of total respiration efflux (Table 2). Leaf litter decomposition accounted for only 3–7% of total respiration efflux depending on the year. Thus, the decaying masticated biomass resulting from shrub removal, thinning and mastication accounted for only a small fraction of total respiration after thinning.

Thinning decreased GEP considerably in 2000 causing it to be 202 g C m^{-2} (14%) lower than in 1999 (Table 2) while the weather was rather similar. In 2001 and 2002, GEP increased along with LAI as the stand recovered from thinning (Table 2). However, in 2001 GEP was still 111 g C m^{-2} lower than the year prior to thinning (1999), while LAI exceeded the pre-thinning level (Fig. 2d) and soil moisture dropped below 10% (Fig. 1b). In 2002, GEP was 315 g C m^{-2} higher than in 1999, while LAI increased rapidly and the shrubs became a substantial component of the ecosystem (Fig. 2d).

3.4. Net ecosystem exchange

Fig. 4 shows the cumulative sum of NEE for each year. In 2000, 2001 and 2002, GEP became larger than R_e and the ecosystem began to store carbon around the beginning of February (~day 35). We computed the sum of NEE outside the growing season, defined as the period between bud swell (~early May, day 125) and partial leaf-off (~late September, day 275) as in Anthoni et al. (1999) (Table 3). NEE outside the growing season can contribute significantly to the
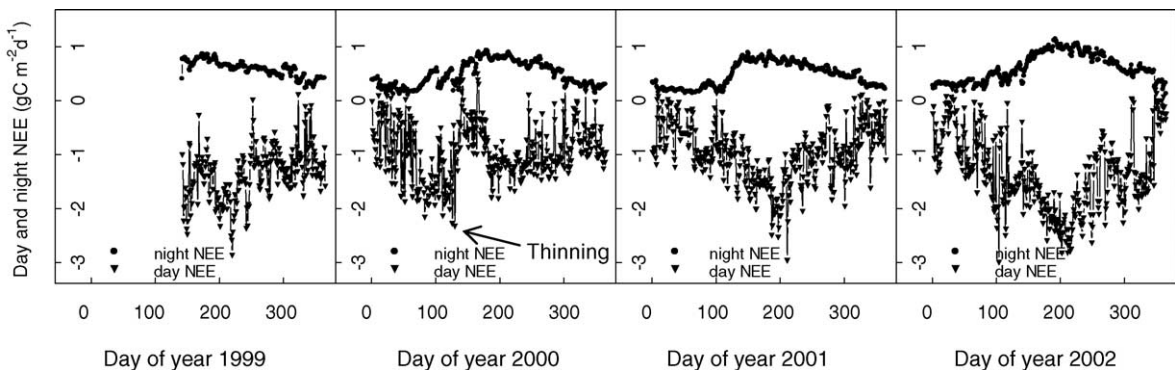

Fig. 3. Mean midday (10:00–14:00) and midnight (22:00–02:00) NEE from 1999 to 2002. Nighttime NEE is modeled R_e (see text).

Table 2
Yearly respiration terms, GEP and NEE from 1999 to 2002

	1999[a]	1999[b]	2000	2001	2002
R_e (g C m^{-2})	938	1261	1273	1254	1604
R_{leaf} (g C m^{-2})	209	249	244	308	405
R_{bole} (g C m^{-2})	47	65	71	104	149
R_{soil} (g C m^{-2})	682	947	949	830	1035
$R_{wood\ decay}$ (g C m^{-2})			8	16	16
$R_{leaf\ decay}$ (g C m^{-2})		42	60	94	45
GEP (g C m^{-2})	−1069	−1462	−1260	−1351	−1777
NEE (g C m^{-2})	−131	−201	13	−97	−172
R_{leaf}/R_e	0.22	0.20	0.19	0.25	0.25
R_{bole}/R_e	0.05	0.05	0.06	0.08	0.09
R_{soil}/R_e	0.73	0.75	0.75	0.66	0.64
$R_{wood\ decay}/R_e$			0.01	0.01	0.01
$R_{leaf\ decay}/R_e$		0.03	0.05	0.07	0.03
$R_e/|GEP|$	0.88	0.86	1.01	0.93	0.90

The ratio of different terms are also shown. $R_{wood\ decay}$ and $R_{leaf\ decay}$ are decomposition fluxes resulting from shrubs removal, thinning and mastication. $R_{leaf\ decay}$ is included in R_{soil} (see text).
[a] Data covering the period from 22nd May to 31st December.
[b] NEE data gap filled using data from 2000 prior thinning.

annual carbon balance of this ecosystem, however, interannual variability is also important. Values ranged from −50 g C m^{-2} in 2000 to 7 g C m^{-2} in 2001 (Table 3). Variations in temperature seem to be correlated with this difference. Fig. 5 shows that midday values of NEE in winter decreased by ~3 μmol m^{-2} s^{-1} when air temperature increased by 10 °C. Coupled to this, average daily air temperature was lower in 2001 and 2002 than in 2000 (Table 3). The frequencies of sub-freezing temperatures were also higher in 2001 and 2002 in comparison to 2000 (Table 3). In addition, sub-freezing temperatures were evenly distributed from January to April in 2001 and 2002, while sub-freezing temperatures occurred mainly

Table 3
Total yearly NEE and NEE outside of the growing season (days 1–125 and days 276–365)

	2000	2001	2002
Total NEE (g C m^{-2})	13	−97	−172
NEE outside of GS (g C m^{-2})	−50	7	3
Mean air, T (°C)	−0.8	−1.5	−2.2
Frequency of $T < 0.0$ (%)	5	12	10

Mean air temperature and frequency of sub-freezing temperature for the period outside of the growing season are given.

between the beginning of January and the end of February in 2000 (data not shown).

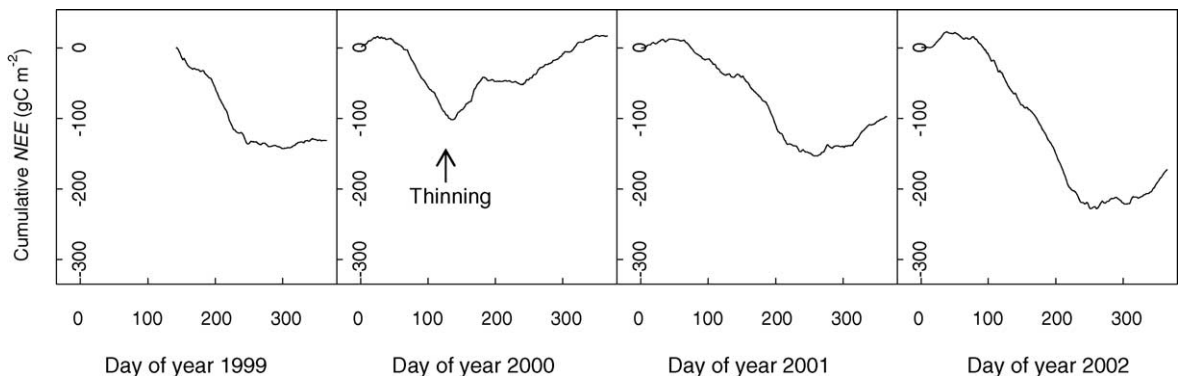In 1999, the ecosystem was storing carbon until the end of October (p3, ~day 300), when R_e became

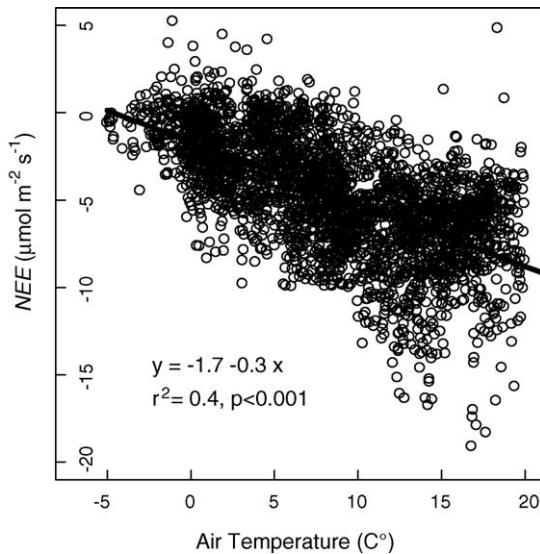Fig. 4. Yearly cumulative sum of NEE from1999 to 2002.

Fig. 5. Relationship between air temperature and midday NEE (10:00–14:00) outside of the growing season (days 1–124 and days 276–365) in 2000, 2001 and 2002 ($n = 3213$).
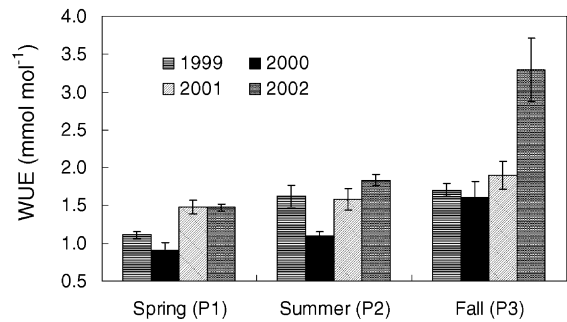

Fig. 6. Mean midday (10:00–14:00) canopy water use efficiency (WUE) for different years and different averaging periods (see text). Error bars are standard errors.

larger than GEP. In 2001 and 2002, the ecosystem began to lose carbon 1 month earlier (mid September, ∼day 260) than in 1999 (Fig. 4), because canopy photosynthesis decreased much faster than R_e after they both peaked in spring (p1) (Fig. 2a and b). In summer (p2) and fall (p3) 2001 and 2002 soil water content was very low compared to 1999 (Fig. 1).

Thinning in spring 2000 changed the seasonality of NEE. As in 2001 and 2002, the ecosystem started to store carbon around the beginning of February (Fig. 4). However, the ecosystem began to lose carbon just after thinning in 2000 because, as we showed earlier, thinning had a greater impact on GEP than on R_e. In 2000, the shift from storage to release of carbon occurred 4.5 months earlier than in 2001 and 2002, and 5.5 months earlier than in 1999 (Fig. 4). As a result the ecosystem was a small net source of carbon in 2000, while it was a sink in 1999, 2001 and 2002 (Table 2). Thinning in 2000 increased NEE by 106% in comparison to the previous year, even though the weather was similar.

3.5. Light and water use efficiency

Water use efficiency showed a slight seasonality with higher values during the growing season (from spring p1 to fall p3) (Fig. 6). The higher WUE follows from a reduction in soil moisture content during the growing season. Thinning had only a small impact on WUE, with a small decrease in spring (p1) and summer (p2) 2000 when compared to 1999 which had a similar climate. A significant increase of WUE occurred at the end of fall (p3) 2002, when the shrubs became an important component of this ecosystem.

Values of light use efficiency (ε_c) were slightly lower in spring (p1) and summer (p2) 2000 following thinning compared to the previous year, even though the values were not statistically different (Fig. 7). ε_c was much higher during fall (p3) 2000 than in 1999, while precipitation input and soil moisture were higher too. ε_c decreased in summer (p2) and especially in fall (p3) 2001 and 2002 compared to the previous years, following a drop in soil water content (Fig. 1b). In all years, ε_c values during the winter (p4) were equal to or higher than those during the other seasons.
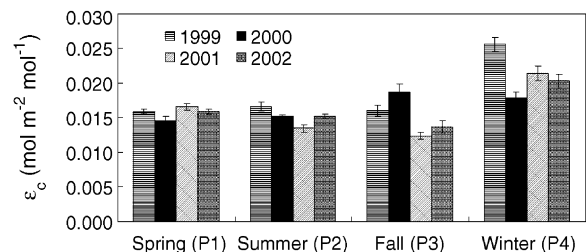

Fig. 7. Mean midday (10:00–14:00) canopy light use efficiency (ε_c) for different years and different averaging periods (see text). Error bars are standard errors.

4. Discussion

4.1. Recovery from clear-cut

This young plantation is still recovering from a major disturbance, the clear-cutting of a mature ponderosa pine forest stand. When we started year-round measurements 9 years after the site was replanted (1999), this ecosystem had already shifted from a net source to a net sink of CO_2. This represents a fast recovery in comparison to published data and simulations for other sites (Law et al., 2003, 2001; Litvak et al., 2003; Thornton et al., 2002; Wirth et al., 2002). In contrast with other sites, Blodgett Forest is characterized by very favorable soil chemical and physical properties, as well as favorable climate for ponderosa pine, which likely accounts for the rapid advance to a net sink of carbon. These factors promote large increases in biomass and LAI from 1 year to the next, influencing the interannual variability of carbon fluxes at our site.

4.2. Climate variability

The annual and the seasonal pattern of rainfall can be very different from 1 year to the next in the Sierra Nevada Mountains of California. Seasonal and interannual climate variability causes significant changes in the fluxes observed through time. During summer and fall, temperatures are high and can drive high rates of ecosystem respiration. However, soil moisture sometimes drops very low and limits soil respiration, as evidenced by the decrease in the contribution of soil respiration to total ecosystem respiration during the two dry years (2001, 2002). This phenomenon has also been observed in other Mediterranean ecosystems (Falge et al., 2002a,b; Reichstein et al., 2002). On the other hand low soil water availability, as recorded in summer and fall 2001, can causes plants to restrict their stomatal conductance and photosynthesis, as also shown at leaf level by Panek and Goldstein (2001). Part of the seasonal and interannual variability of water and light use efficiency is affected by water availability: low soil moisture as in summer and fall 2001 and 2002 was correlated with an increase in the ability of this ecosystem to conserve water (higher WUE), while light use efficiency decreased. These results at

ecosystem level confirm data collected at leaf level (Misson et al., 2004; Panek, 2004). Finally drought stress, like experienced in summer 2001 and 2002, seems to impose more limitation on carbon assimilation than on respiration, and the decline in soil moisture can trigger an earlier shift ($\sim$1 month) of the ecosystem from a carbon sink to a source.

Winter air temperatures are not usually a strong limiting factor for photosynthesis at this altitude (1315 m) of the Sierra Nevada: midday mean temperature in winter usually varies between 0.0 °C and 10 °C. Furthermore, soil temperature data indicate that the soil is rarely frozen (data not shown) and soil water content is high. Needles are able to respond effectively to incoming radiation as it increases in February after a minimum in January. This is confirmed by the high level of canopy light use efficiency that we recorded during the winter. In addition, the only contributor to the CO_2 efflux out of the ecosystem during this period is maintenance respiration. Thus, significant net carbon uptake can take place outside of the growing season, as observed in other sites dominated by evergreen foliage in mild winter climates (Anthoni et al., 1999; Falge et al., 2002b; Law et al., 2000a,b; Morgenstern et al., 2004). Large interannual variations in NEE outside of the growing season are associated with canopy photosynthesis responding to differences in the intensity, frequency and temporal patterns of low winter temperatures. During spring, flux variability is associated with the timing of increasing temperatures. Data from 1997 and 1998 shows that differences in spring GEP between years can account for 20% of total yearly GEP (Goldstein et al., 2000).

4.3. Thinning and shrub removal

Interannual variability in the carbon fluxes at our site was strongly influenced by anthropogenic disturbances, e.g. shrub removal and thinning/mastication. The removal of shrubs in 1999 and their reemergence in 2002 not only changed the biomass and the LAI of the stand, but also represented a shift in species. Data collected in 2003 showed that photosynthetic capacity of Ceanothus and Arctostaphylos leaves can be three times higher than that of ponderosa pine on a leaf area basis (data not shown). Consequently, the shrubs provided a small contribution in

terms of leaf surface area but contributed greatly to the amplified canopy scale uptake of CO_2 when they reappeared in 2002. It is likely that this shift in species influenced also part of the variability in the water use and light use efficiency of the ecosystem: both properties increased in 2002 in comparison to 2001 while the climate was rather similar. The shrub removal and reemergence clearly caused the CO_2 fluxes to vary significantly, but also caused a substantial change in the general functional properties of the stand.

In several cases, thinning has been shown to increase soil temperature and soil moisture, which lead to increasing rates of soil litter decomposition and mineralization (Dewar and Cannell, 1992; Thibodeau et al., 2000; Vesterdal et al., 1995). These effects, plus adding harvest residues, have been thought to increase soil CO_2 efflux to the atmosphere. Indeed, Ohashi et al. (1999) showed that thinning increased soil respiration by 40% in a *Cryptomeria japonica* stand in Japan. However, Striegl and Wickland (1998) showed that soil respiration decreased by 40% after clear-cut in a *Pinus banksiana* stand in Saskatchewan. Several studies based on eddy-covariance measurements have also shown that clear-cutting or wind throw decreased soil and ecosystem respiration (Amiro, 2001; Knohl et al., 2002; Kowalski et al., 2003; Rannik et al., 2002; Striegl and Wickland, 2001).

Our results showed that soil and total ecosystem respiration were not significantly affected by thinning and mastication because of compensatory effects. Impacts of thinning on soil respiration at our site have been thoroughly discussed in Tang et al. (2005). The model developed in that paper showed that soil respiration decreased by 13% after thinning at a given soil temperature and moisture content. Thus, the decrease in soil CO_2 efflux due to the reduction in root respiring biomass was not totally compensated by the increase in decomposition of dead roots after thinning. However, soil temperature and moisture also increased slightly after thinning (Tang et al., 2005), causing soil respiration to be almost equal in 1999 and 2000. Aboveground respiration was unaffected by thinning because the loss of respiring biomass by thinning in spring 2000 was largely compensated for by the increase of leaf and stem biomass later during the summer of the same year. In addition, the contribution of wood and leaf debris decomposition to the total efflux out of the ecosystem was negligible.

Thinning did significantly decrease the amount of CO_2 assimilated through canopy photosynthesis because of the reduction in leaf assimilating surface. However, water use and light use efficiencies of the foliage were not modified significantly in the short term. Mainly due to this change in GEP, the ecosystem became a source of CO_2 to the atmosphere, consistent with published results for other type of disturbances such as clear-cutting or wind throw (Amiro, 2001; Knohl et al., 2002; Kowalski et al., 2003; Rannik et al., 2002; Striegl and Wickland, 2001). However, in contrast to these cases, recovery from disturbance was much faster for thinning at our site; the ecosystem was again a sink of carbon only 1 year after the mastication. This is partly because thinning is a partial disturbance. Such fast recovery was also likely related to the favorable site factors and juvenile attributes of the trees. In the case of more mature stands and/or more limiting soil and climate the recovery could be slower.

As previously stated, thinning is used for several purposes including timber harvest, tree growth redistribution, improvement of biodiversity and forest health, and wildfire-hazard reduction. Since forests are one of the main components of the terrestrial carbon sink, they could also be managed for carbon sequestration (Houghton, 2003; Schulze et al., 2003). We have shown that thinning and mastication converted this young plantation from a sink to a source of CO_2 for a very short time. Applying thinning as a management practice at a juvenile stage of this plantation allowed the trees to react vigorously and the ecosystem to recover quickly from this disturbance. How the ecosystem will respond in the long term is unresolved. A simulation study by Thornton et al. (2002) suggested that there should be an early pattern of carbon source followed by a strong and gradually diminishing sink during recovery from a major disturbance. Their simulation showed that the timing and magnitude of fluxes following disturbances depends on disturbance type and intensity, and on post-disturbance management treatments. In the long term, decomposition of dead material (root, wood, leaf) will have a minor effect on the carbon balance of our site because management practices produced a relatively small quantity of debris (496 g C m^{-2} of

wood and leaf, plus dead roots biomass that were not estimated). This quantity is much smaller than that from disturbances analyzed in other studies such as wind throw (7240 g C m^{-2}, see Knohl et al. (2002)). The long-term impact of thinning on the carbon balance will be driven mainly by the ecophysiological effects of this practice, linked to the change in microclimate and the modification of intra- and inter-species competition. On a decadal time scale, two studies focusing on thinning effects on net primary productivity showed that thinning increased total above-ground biomass production (Mitchell et al., 1996; Mund et al., 2002).

In the Sierra Nevada, products of precommercial thinning are left on site, and mastication is applied to reduce fire-hazards (Graham et al., 1999). The impact of thinning and mastication on the carbon balance of these stands should be compared to the major alternative: wildfire that sometimes causes a loss of CO_2 to the atmosphere corresponding to the total biomass of the stand. Furthermore, as growing stocks in forests are expected to increase with future global change, recent studies have suggested that the forest carbon sink is likely to become smaller (Karjalainen et al., 2003, 2002). Natural disturbances may be more frequent if forest management and felling of trees remains unchanged (Schelhaas et al., 2003, 2002). In the Sierra Nevada, management practices have been adapted by increasing the area thinned each year; however, the new management plan proposes to remove only about 25% of the forest increment per year (USDA, 2004). Even with this new plan, the increase in biomass could be a serious concern.

5. Conclusion

In this paper, we showed that a large number of factors controlled the seasonality and the interannual variation of carbon fluxes in a young ponderosa pine plantation located in the Sierra Nevada of California: recovery from past disturbance (clear-cut), climate variability, changes in species composition, and forest management practices, e.g. shrub removal and thinning. The response to these factors was affected by the juvenile attribute of the trees and favorable site factors. Thinning dramatically reduced canopy photo-synthesis while ecosystem respiration was not significantly changed due to compensatory effects. Ecosystem water use efficiency and canopy light use efficiency were not particularly affected by thinning, but their seasonal and interannual variations were sensitive to phenology and climate variability. Overall, thinning had significant impacts on the magnitudes of net carbon fluxes, with the most striking effect being a conversion of the ecosystem from a sink to a source of CO_2 in the short term. One year after thinning, this ecosystem was again a strong sink of carbon. The long-term effects of thinning are still uncertain and would require additional years of measurements to elucidate.

Forest management practices are expected to change globally in the coming decades, towards an increase in the area and the intensity of thinning. In this context, our results suggest that the impact of management practices on carbon and energy fluxes is important, and must be included in biosphere models in order to improve estimates of terrestrial carbon budgets. Furthermore, in certain regions increasing the area and the intensity of thinning may decrease the impact of natural hazards such as wildfire.

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